

A Dangerous Idea in Zoology: Ignoring the Role of Genetics in Biodiversity Restoration

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ABSTRACT

The term 'biodiversity' emerged in the mid-1980s and quickly became sufficiently popular that it could have been viewed as a 'new field of science'. The broader community has also embraced the term and, ultimately, it has become a proxy for species conservation. As a consequence, conservation of biodiversity has effectively become the only approach to minimising continued species loss. However, despite the widespread use of the term, there is confusion over its definition, even among disciplines to which the term has become a focus. In Australia, much of the biodiversity conservation/restoration is community-driven (e.g., landcare, political pressure of animal welfare groups) with a focus on species and habitat biodiversity. Genetic diversity is seldom seriously considered. As a consequence, native species biodiversity management is often not maximising the potential outcomes. Arguably the greatest issue associated with incorporating genetics more centrally into biodiversity restoration is that its definition is often considered complex. In addition, the negative aspects of ignoring the genetic component of biodiversity may be masked by the positives when the outputs of a program provide many individuals of species considered at risk of extinction despite the longer term outcomes potentially having the opposite effect. To better manage biodiversity restoration all of us who use the term within our discipline need to ensure that, wherever possible, we seek to inform those around us of the importance of genetic biodiversity in biodiversity restoration programs. A first step is to determine a simple, all-encompassing definition of biodiversity that explicitly includes genetics.

Key words: definition of biodiversity, single-species management, species diversity, community-driven ecological restoration, koala conservation, endangered species restoration

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Introduction to 'biodiversity'

'Biodiversity' emerged as a term in the ecological literature in the mid-1980s and, within a decade, it had become so popular that it could have been viewed as a 'new field of science' (Ghilarov 1996). Subsequently, there has been a 'steady increase' in the use of the term, and particularly since the 1992 United Nations Earth Summit Conference in Rio de Janeiro (Loreau *et al.* 2006), evidenced, for example, in the title of scientific articles (Kaennel 1998; Loreau *et al.* 2006). However, despite the concept having become entrenched in both the academic and the general language of the broader community¹, the term 'biodiversity' continues to be identified and evaluated differently at all levels of society, internationally and nationally, and among organisations, local communities, and even among researchers from different disciplines - genetics, botany, anthropology, economics (Kaennel 1998; Ewers and Rodrigues 2006; Caillon and Degeorges 2007).

Norton (2006) suggested that defining biodiversity appropriately was important because of its role as a 'proxy' for species conservation, and because it is effectively the only approach being considered in the minimisation of continued loss of species. Further, he also suggested that it was by no means a trivial task to define 'biodiversity'. This

is because, in addition to the incorporation of ecological attributes within the definition, it also has to be considered in terms of social goals and values. Using the United States of America's (USA) Endangered Species Act 1973 as an example, Norton (2006) pointed out that social values were central to biodiversity conservation in that Act. It actually identifies the 'social values' of aesthetics, education, historical, and recreation, together with ecological and scientific attributes. As a consequence, it was suggested that any definition of biodiversity needed to span both 'policy discourse' and 'biological respectability'. To achieve this outcome, it was suggested that a 'bridge term' was required that 'linked discourse about policy goals to scientific data and theory, all within a discourse associated with policy choices' (Norton 2006, p. 50).

The Australian Environment Protection and Biodiversity Act 1999 is the Federal Government's 'central piece of environmental legislation'. Its emphasis is different in some respects to that of the USA's Endangered Species Act in that the focus of the Federal legislation, and thus the states and territories, provides 'a legal framework to protect and manage nationally and internationally important flora, fauna, ecological communities and heritage'. If it is assumed that this

¹ At the end of September, 2014, the key word 'biodiversity' on 'Google' elicited 52,000,000 hits, and 'Google Scholar' 1,300,000.

reflects Australian community values, the emphasis is on endangered species and ecological communities and not *per se* biodiversity.

'Defining biodiversity'

As Norton (2006) acknowledged, the definition of the word 'biodiversity' is complex and, together with others (e.g., DeLong 1996; Ewers and Rodrigues 2006; Holt 2006), he suggested that even within the scientific disciplines that embrace biodiversity as a core of their discipline there was a lack of consensus over the definition of the term 'biodiversity'. For example, when Takacs (1996) undertook in-depth interviews of what he considered to be the most active of the biological advocates for biodiversity in the world, he asked each of them to define the term. He reported that the answers differed greatly. This, in part, reflected what Wood (2000 p. 41) argued was a major dichotomy in the definition of the word. He characterised one of the alternatives in this dichotomy as 'biological entities that are different to one another' and the other as the 'differences among biological entities'. The former emphasised the entities involved while the later focus has been on 'an environmental condition or state of affairs relative to the entities'. As an example he explained that using the inventory perspective of his dichotomy, the emphasis would be focused on the sum total of taxa. This would not incorporate any form of weighting where one species was more valued than another. In contrast, the alternative form of the definition in this dichotomy favoured taxa that were unique (e.g., a species without close relatives). The relative novelty of the taxon would thus have importance under the latter, but not under the inventory definition. Takacs (1996, p. 47) found that others defined biodiversity as 'the product of organic evolution'. This definition incorporates the 'diversity of life in all its manifestations' and thus emphasises both the processes and the products of the processes and, although not necessarily explicit would include genetic biodiversity.

As the foregoing dialogue indicates, the definition of biodiversity may appear ambiguous even among the professionals that are leaders in the field, and governments. For example, the definition of Sarkar and Margules (2002), 'biodiversity is the variety of life' is typical of a definition that could either be assumed to simply be referring to species level diversity (i.e., the most familiar), or applied more broadly and thus encompass, among other attributes, the genetic biodiversity. However, it is my view that it is a 'dangerous idea' not to be at least as explicit in defining genetic biodiversity as E.O. Wilson was when he defined biodiversity, albeit restricted to inventory attributes of biodiversity, as 'the variety of life across all levels of organization from genic diversity within populations, to species, which have to be regarded as the pivotal unit of classification, to ecosystems. Each level can be either treated independently or together as a total picture. And each can be treated either locally or globally' (Takacs 1996, p. 50). However, even within

such a detailed definition the reader is provided with² the benefit of choosing the level of diversity (and presumably ignoring others) as Wilson says 'each level can be ... treated independently ...'. Most definitions have been coined in the inventory style of Wilson (Takacs 1996). Others, such as Wood (2000, p. 41), define biodiversity as the 'sum total of the differences among biological entities'. It is not surprising, therefore, that the term has often become restricted in common usage to only the most familiar aspect of biodiversity – the species level.

The focus of Australian environmental legislation could be considered to be within the 'novelty' realm of biodiversity definitions, albeit with the emphasis on endangered species rather than taxonomic uniqueness. However, this definition is not entirely restricted to threatened species conservation *per se* but also incorporates the novelty that encompasses 'endangered ecosystems' (e.g., Cumberland Plain Woodlands - DECCW 2011) and, although the human aspects of the USA act that Norton (2006) described are not enshrined in the Australian environmental legislation, the community tends to drive restoration decisions, often without a clear understanding of the ecological underpinning required (e.g., Burgin *et al.* 2005; Saunders 2007).

Community driven decision making in restoration ecology

Beyond the formal legislative instruments, Australian governments' management approach to biodiversity restoration encourages community-driven conservation. This is despite, as pointed out above in the comparison of the USA and Australian legislative approach, such consideration has not been made explicit in the aims of the legislation. Instead the agenda is often driven by political backlash over decisions made that have been based on ecological information (e.g., koala management, Kangaroo Island - Duka and Masters 2005; kangaroo cull – Australian Capital Territory reserves – Cox and Thistleton 2012; Jean 2013) or through governments' support of community landcare that does not explicitly include the need for ecological input (see e.g., Burgin 2002; Lunney and Burgin 2002).

Under the banner of 'Landcare', there are over 4,000 Landcare and 2,000 Coastcare groups and 'many thousands' of volunteers (i.e., 'everyone, everywhere, landcare') in partnerships with governments, communities, and organisations that claimed to care for the 'natural resources' of Australia. Their activities include planting 'millions of trees', and restoration of wildlife habitats (Landcare Australia undated). In an Australian-wide survey of these care groups, 82.5% claimed that their overall aim was to 'help protect the

² The Federal Government's Environment Protection and Biodiversity Conservation Act, 1999 (Section 17(13) defines biodiversity to include '... species, habitats, ecological communities, genes, ecosystem and ecological processes' (EPBC 1999).

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local environment for future generations'. However, almost half (47.5%) of the groups also claim that their aim was to 'educate and inform people about natural resource management'. Despite this, on a scale of 0-5 (5 least important), only the need for 'tools and equipment' had a lesser priority (4.27) than either 'training to build skills and capacity' (4.17) and information on 'e.g., best practice, issues, events and government policies' (4.16). The most common group activity (60.8%) was 'planting and weed management' (Landcare Australia 2011). There was, therefore, no evidence that scientific knowledge was viewed as valuable in the support of biodiversity restoration within this network of volunteers. Based on the data from this Landcare Australia survey, working within ecological restoration (formally and informally), and my role with the peak body of catchment management in New South Wales for over a decade (see e.g., Burgin 2002; Lunney *et al.* 2002), together with my previous research (e.g., Burgin 2002; Burgin *et al.* 2005), there is little doubt in my mind that if there were a consensus definition of biodiversity among landcarers it would be heavily focused on 'community biodiversity', often without what most ecologists would view as a clear understanding of the concepts the groups seek to incorporate into their restoration activities³.

The most broadly disseminated definition of biodiversity within Australia outside of the research community would, therefore, be strongly focused on community and species level biodiversity associated with threatened and endangered species/communities (albeit strongly focused on tree planting), with limited concern for the genetic level diversity or ecosystem services attributes of biodiversity. For example, Burgin *et al.* (2005) surveyed Landcare groups in the Hawkesbury-Nepean Trust Area of New South Wales on the use of local provenance (cf. genetic stock) in their planting activities. Of 85 Landcare groups, 20% were not aware of genetic diversity, despite having the stated aim of restoring biodiversity. A substantial number of other groups who claimed they considered local provenance (genetic biodiversity) in their landcare activities, when questioned about the source of their seed/seedlings demonstrated that it was not a priority. All indications were that genetic diversity was generally not an important consideration and certainly not an overarching one. This widespread lack of concern for genetic biodiversity can be traced to a lack of acknowledgement in definitions of the need and/or value of its consideration in biodiversity restoration.

Biodiversity restoration in the 'Utopian terminology world'

In the 'utopian terminological world' a term and the associated concept would be substantiated (Kaennel

2008). However as Kaennel (1998) attested this has not often been a reality and, as outlined above, is definitely not the situation with the term 'biodiversity'. Currently, this term is being interpreted in different ways in different contexts to the point where it has become a 'buzzword' and thus often misleading rather than informative. Recognising these issues, Kaennel (1998) suggested that, adjudicated by 'a panel of judges', more context-specific specialist terms should be developed for different attributes of 'biodiversity' that are currently considered to be included in the term, although not necessarily in any given situation. However, given the experience of those who have interviewed leaders in the field (e.g., Takacs 1996; Erwers and Rodrigues 2006), I suggest that there is unlikely to be consensus since these scientists only represented the 'experts' in the broader academic community that consider the term as a part of their vocabulary, and not the broader community.

With the knowledge that there is no clear definition of 'biodiversity', the obvious question is 'does it really matter in the restoration of biodiversity?' I believe that in ecological restoration, the development of definitions of biodiversity ignoring the concept of genetic biodiversity is a 'dangerous idea'. However, despite an on-going and widespread focus on biodiversity restoration which is typically focused on species and wildlife habitat (McKay *et al.* 2005), together with an on-going expansion of associated fields of study (e.g., Lindenmayer and Hobbs 2007; Howell *et al.* 2012; Hobbs *et al.* 2013), there is limited understanding of the role of genetics in ecological restoration (Knapp and Dyer 1998; Jones 2003; McKay *et al.* 2005).

In the context of plant communities, T. J. Whittaker (1960, 1975) coined the phrase 'diversity begets diversity' to describe that diverse elements that undergo diverse processes will generate higher levels of diversity. The alternate is that losses of biodiversity can be expected to result in further losses.

During reproduction when genes recombine, the outcome is the release of genetic and phenotypic variability that underpins adaptive change (Lewontin and Birch 1966; Arnold 2006; Arnold and Martin 2010). It follows therefore, that lower genetic diversity within a population will result in less opportunity for such variability and thus enhance levels of inbreeding (i.e., inbreeding depression, lowered heterozygosity/greater homozygosity). Such outcomes present a higher risk of local species' extinction, particularly where habitats are isolated and/or fragmented (Dunham *et al.* 1997; Fahrig 2002; Újvári *et al.* 2002). For example, Újvári *et al.* (2002) proposed that low genetic diversity, a result of inbreeding depression, was a major cause for the endangerment of Hungarian populations of the Hungarian meadow viper *Vipera ursinii rakosiensis*. In Australia, the brush-tailed rock-wallaby *Petrogale penicillata* is critically endangered in Victoria. Browning *et al.* (2001) found that each of the State's populations had low genetic variability

³ It should be noted that not all Landcare 'restoration' is focused on biodiversity restoration *per se* but rather groups may be focused, for example, on restoring other degradation problems such as salinity. It is, therefore, inappropriate to assume that they are focused only on restoration of biodiversity.

within each of its isolated populations, and that each population carried alleles that were unique to that specific population. These findings are typical of random genetic drift that results from random loss of genetic diversity and associated fixation of a single genotype (or at least a reduced number of genotypes) within isolated populations. This is a phenomenon that has been widely observed in small populations (Frankham 1998; Frankham *et al.* 2004; Sanders and Bowman 2012). Such loss of genetic diversity has been demonstrated to be significantly associated with a reduction in fitness due to inbreeding (Reed and Frankham 2003). These phenomena have been demonstrated to be most marked in small populations (e.g. Újvári *et al.* 2002; Reed and Frankham 2003), including endangered species (brush-tailed rock-wallaby *P. penicillata* - Browning *et al.* 2001; northern hairy-nosed wombat *Lasiorhinus krefftii* - Taylor *et al.* 1994, 1997) and/or in species that have otherwise been subjected to genetic bottleneck/s (Frankham 1986).

Probably the most widely studied free-living populations in regard to the bottleneck phenomena are island populations (Frankham 1998). In a comparison of 202 island populations with their 'mainland counterparts', Frankham (1998) found that 81.7% of the island populations had lower heterozygosity (i.e., genetic variability) than their mainland counterparts. Fragmented, isolated, mainland remnant habitats where wildlife have limited (if any) ability to migrate typically mimic these island habitats. The same impacts may, therefore, occur that have been evidenced in fragmented *P. penicillata* populations by Browning *et al.* (2001).

In the context of restoration of biodiversity, any phenomenon which is a consequence of a small 'founder population', whether the species is native or exotic, will result in a genetic bottleneck. In the extreme, a population may be founded on the basis of a single inseminated (or pregnant) female, particularly since sperm storage is an integral part of the reproductive cycle in many species (Neubauer and Wolfner 1999). For example, classified among the 'top 100 invasive species worldwide' by the International Union for the Conservation of Nature/Species Survival Commission (IUCN/SSC 2009), *Trachemys scripta elegans* red-eared slider turtle, an introduced species to Australia, may produce fertile offspring for up to five years post-insemination with multiple clutches annually that may include more than 20 eggs (Burgin 2006). At least theoretically, a population may, therefore, be based on just one 'escaped' pregnant female. This would generally result in an extreme genetic bottleneck.

Genetic bottlenecks may also occur due to population declines in a species natural habitat, translocation, founding effects and/or introductions. Each of these phenomena has occurred with the koala *Phascolarctos cinereus*; however, unlike many other species, they have been well documented for the koala. Over

European history this species has undergone dramatic oscillations in abundance with local extinctions and range reductions (Reed and Lunney 1990). Houlden *et al.* (1996) observed that the pattern of genetic diversity reflected the history of translocations. Although reduced in number post-European settlement, in the northeast of Australia, koalas were considered common when hunting ceased due to the species' protection in the 1930s (Barrett 1943), and they have recovered without large-scale manipulation (Reed and Lunney 1990). Conversely, Lewis (1934) considered that they were extinct in South Australia and near-extinct in Victoria when hunting became illegal. This revelation sparked major restocking programs which included introductions (sometimes multiple introductions) to islands in Westernport Bay and the Bass Strait. At least on occasions, these populations were founded on very few individuals that had already previously been through genetic bottlenecks. Subsequently, individuals from the islands were reintroduced to the mainland and to Kangaroo Island (for documentation of introductions and translocations see Houlden *et al.* 1996). Genetic diversity was found to be higher in northeast Australia than in the southeast, and lowest on Kangaroo Island. These outcomes parallel the history of manipulation of koala populations across these areas (Houlden *et al.* 1996; Lee *et al.* 2009).

Genetic bottlenecks are not restricted to the introduction or translocation of small numbers of individuals *per se*. However, the origin and diversity of the genetic stock used for translocation may actually extenuate the number of bottlenecks that the population will proceed through, and thus loss of heterozygosity. As has historically occurred with koalas, translocated individuals have often been sourced from island populations (e.g., Houlden *et al.* 1996; Melzer *et al.* 2000; Phillips 2000; Lee *et al.* 2010). For example, Houlden *et al.* (1996) reported that koalas for translocation had been sourced from island populations that were the descendants of a few individuals that had originally been introduced to the island from wild populations of the mainland and sometimes even re-translocated to other islands. This has resulted in multiple genetic bottlenecks, and presumable loss of genetic diversity in the translocated populations (Houlden *et al.* 1996; Lee *et al.* 2010).

An alternative to translocating free-ranging animals, particularly those that have already declined in the source population, has been to instigate captive breeding for later release. Historically, these individuals may be captured from a restricted area of the species' range (i.e., presumably a sub-set of the genetic diversity available across the population) and, on other occasions where a species was on the brink of extinction (e.g., *Tricholimnas sylvestris* Lord Howe Island woodhen - Miller 1985) it is, at best, effectively the remaining genetic diversity for the species. For example, in the case of the Lord Howe Island woodhen, by 1980, the maximum number of

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breeding pairs was 10, all located in remote areas on the island's highest mountain peaks and thus assumed to be inbred individuals at each site, and since the species was widespread and common at human contact, presumably a small sub-set of the previous genetic diversity of the species. There had been high adult mortality among breeding females between 1978 and 1980 when adult deaths exceeded recruitment into the population. In 1980 only three healthy pairs of woodhens remained. Because breeding was reduced to these six individuals, they were used as the basis of the captive breeding colony to produce individuals for reintroduction into the wild. They effectively represented the genetic future of the population and thus from the beginning the genetic welfare of the species was compromised (Ballou *et al.* 2010). By 2007, the population of Lord Howe Island woodhens numbered 200 (DECC 2007).

As with the Lord Howe Island woodhen, Leberg and Firmin (2008) reported that a 'common feature' of captive breeding populations is that they are based on a small number of founding individuals.

This may occur, even when the resources are available to establish larger breeding populations. An additional issue with a small founding population is that the smaller the number of individuals available for captive breeding the more likely it will be that the matings will be between related individuals. Frequently, the source of such animals for captive breeding are island populations that typically have lower genetic diversity than mainland populations (e.g., dibbler *Parantechinus apicalis* – Mills *et al.* 2004; koala – Houlden *et al.* 1996; Melzer *et al.* 2000; Phillips 2000).

Captive populations are also exposed to additional genetic bottlenecks because not all genotypes are successful under captive conditions. Under such circumstances, inbreeding depression will result in a reduction in mean population fitness and expose the population to the threat of reduced viability. This problem is increasingly an issue as the number of founders is reduced (Frankham 1995a; Hedrick and Kalinowski 2000; Spielman *et al.* 2004). One reason for this is that inbreeding exposes selection to the deleterious, recessive genetic characteristics that the population carries. This process, referred to as purging, reduces the frequency of deleterious genes within the population and thus may also reduce inbreeding depression (Crnokrak and Barrett 2002; Glémin 2003; Leberg and Firmin 2008). However, while recognising the role that inbreeding depression has on the expression of deleterious genes in a population, Frankham (1995b) suggested that the negative effects of purging in small populations have been overestimated. No matter what the outcome, an inbred population is subjected to a genetic bottleneck at this stage of the captive breeding cycle with further genetic bottlenecks due to, for example, release from captivity into the wild. These effects were observed by Woodworth *et al.* (2002). They investigated populations of *Drosophila* sp. of different densities that were maintained

under 'benign captive conditions'. After 50 generations fitness was reduced in their small populations as a result of inbreeding depression but in large populations there was a small increase in heterozygosity due to 'modest' genetic adaptation. When these flies were introduced to 'wild conditions' the reproductive fitness of all 23 populations declined substantially (64-86%) compared to control populations. Release of these individuals to 'wild conditions' therefore imposed another substantial genetic bottleneck on the captive population.

These are not the only genetic bottlenecks that the captivity bred populations face. As already alluded to, some individuals will be better adapted to captive conditions than others, and thus produce proportionately more offspring. In addition, Leberg and Firmin (2008) suggested that when the number of captive individuals is sufficiently large for release, typically only a small number is released in any one episode – usually resulting in an additional genetic bottleneck. As Woodworth *et al.* (2002) observed, different individuals released into the wild respond differently. Generations of individuals from the same source stock will; therefore, likely result in a skewing of the population towards some sub-set of the genetic diversity that survived these multiple bottlenecks. As a consequence genetic deterioration in captivity may be a major problem in long-term captive breeding programs, and even for the wild populations that the captive animals have been released into over future generations.

Other factors that may influence captive breeding success include disease outbreaks, establishment of self-sufficient captive populations, domestication, maintaining administrative continuity, and the substantial costs of the operation (Snyder *et al.* 1996). In addition to the issues of poor success rates due to reintroductions (Snyder *et al.* 1996; Woodworth 2002), Snyder *et al.* (1996) also voiced concern that captive breeding was becoming increasingly popular, and thus may pre-empt alternative recovery techniques. They considered that captive breeding should not be 'invoked prematurely' and such programs should not be introduced to recovery programs before appropriate evaluation of all alternatives, and before it had been determined that captive breeding was necessary for the survival of the species. It was recommended that captive breeding should be introduced only as a 'last resort' in a species recovery plan after all other effective, short term options were exhausted.

Such a situation has apparently occurred with the two Australian species of corroboree frog (*Pseudophryne corroboree*, *Pseudophryne pengilleyi*). Until 1966 both species were considered abundant (Colefax 1956; Pengilley 1966) but both species have subsequently declined, and by 2008 it was predicted that the two species were critically endangered and could be extinct in the wild in three years (Morgan *et al.* 2008). In 2013 no corroboree frogs were found during the annual census.

The major cause of the decline coincided with the chytrid fungus *Batrachochytrium dendrobatidis* and the decline of other species within the Southern Alps (Hunter 2007, Hunter *et al.* 2009). Genetic analysis across the range of both species indicated that heterozygosity in the remnant wild populations remained high (Morgan *et al.* 2008). Captive breeding/husbandry was introduced for the species. Eggs of the northern corroboree frog have been collected and reared in captivity to mature frogs and ultimately they will be released to the wild. It is also planned to maintain a 'self-sustaining (breeding) captive population' as insurance against the ultimate extinction of both of these species in the wild (ESDD 2014). Taronga Zoo (Sydney) introduced a breeding program for the southern corroboree frog with ultimate release of offspring to the wild. In 2013 the program was extended to trial the release of eggs and tadpoles into enclosures within the species' range (TCSA 2013). If successful, this will potentially reduce some of the bottleneck effects due to captive breeding although not all of them. In the face of on-going decline and critical endangerment of these species, caused (at least in part) by disease (Hunter 2007; Hunter *et al.* 2009), there is presumably no other apparent avenue to immediately overcome the ultimate extinction of the species. Captive breeding would thus, presumably, have been an example of the 'last resort' that Snyder *et al.* (1996) identified. The captive breeding of the Lord Howe Island woodhen was another such example since the population was effectively functionally extinct with the few remaining adults being lost at a faster rate than replacement (Miller 1985).

Witzenberger and Hochkirch (2011) surveyed the literature that focused on the molecular genetics of captive breeding of endangered animal species. The majority of the studies (70%) reported on specific breeding programs, and these showed a 'marked bias' to a few species. The most studied were carnivores (25%), ungulates (26%), birds (19%), primates (9%), and reptiles (9%). The authors concluded that the genetic impacts of captive breeding varied substantially due to a range of factors. Overall; however, there was a strong correlation between genetic diversity, size of founder population, and the size of the captive population. It was concluded that to minimise inbreeding there should be a minimum of 15 individuals in the founder population, and at least 100 in the captive population. Individuals in the founder population should also not be related, and new founders should be integrated into the population successively.

While effective population size in a breeding colony is clearly of importance, the identity and number of founders (i.e., genetic makeup) that contribute to the captive breeding program also has a major determining effect on the genetic diversity (Witzenberger and Hochkirch 2011). For example, Laikre and Ryman (1991) found that although it was previously reported that mammalian carnivores and other species with similar social structures were adapted to close inbreeding, they found that the wolf

Canis lupus bred in Scandinavian zoos presented with the effects of inbreeding that included a reduction in juvenile weight, low reproduction, reduced longevity, and blindness. The varying traits observed were linked to genes originating from different founding pairs, and it was predicted that such traits would affect fitness within the population.

As indicated above, one of Witzenberger and Hochkirch (2011) findings was that population fitness was improved when new founders were successively integrated into captive breeding populations. Spielman and Frankham (1992) provided evidence that even one immigrant into a small isolated captive population of *Drosophila melanogaster* approximately doubled the reproductive fitness of the population.

It is not necessarily the captive breeding environment *per se* that creates genetic bottlenecks in biodiversity restoration. The factors outlined above that may impact on captive populations, may also occur in free-living, isolated populations including island or isolated and/or fragmented mainland sites (e.g., dibbler *Parantechinus apicalis* - Mills *et al.* 2004; koala - Houlden *et al.* 1996; black-footed rock-wallaby *Petrogale lateralis* - Eldridge *et al.* 1999; brush-tailed rock-wallaby - Browning *et al.* 2001, Taggart and Houlden *et al.* 2001; northern hairy-nosed wombat - Taylor *et al.* 1994, 1997). For example, Eldridge *et al.* (1999) observed that island populations of the black-footed rock-wallaby suffered from inbreeding depression that included reduced fecundity in females, a skewed sex ratio, and increased levels of fluctuating asymmetry. Seymour *et al.* (2001) also observed the effects of inbreeding suppression in free-ranging koalas that had been through sequential founding events in recent history. The incidence of testicular aplasia was positively correlated with effective inbreeding coefficients derived from heterozygosity values, and was undetected in a non-bottlenecked population they studied.

As other researchers had previously reported (e.g., Franklin 1980; Lande 1995; Woodworth *et al.* 2002), Witzenberger and Hochkirch (2011) recommended that when the goal for captive breeding colonies is to retain evolutionary potential (as should be the situation in biodiversity restoration programs), the population size should be substantially larger than the 100 that they recommended as the minimum size. However, even among the *ex situ* populations managed by the Associations of Zoos and Aquariums, Baker (2007) reported that 67% had a population size of less than that which Witzenberger and Hochkirch (2011) identified as being the minimum number required in most situations that they investigated – some required larger population sizes. As previously indicated, small founder populations and/or effective population size may exacerbate the issues associated with inbreeding. For example, it was suggested by Ralls and Ballou (1986) that such populations are 'likely' to become extinct due to chance events including a succession of births of one sex, disease, and/or genetic

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problems. For example, they reported that across 45 mammalian populations (8 orders, 37 genera), juvenile mortality of inbred young was higher than non-inbred young in over 90% of populations.

As previously identified, sequential bottlenecks occur within captive breeding populations. Over time these may result in changes in behavioural and physiological traits that have allowed specific lineages to prosper in captive breeding conditions but, in turn, prove detrimental in natural situations. This is because the two environments are very likely 'radically' different. In this context, Lynch and O'Hely (2001) suggested that managers of an endangered species population face 'double-jeopardy'. Failure to intervene when confronted with species decline may result in the species' extinction. Conversely, genetic changes in the captive environment may reduce the potential for these same individuals to cope under natural conditions since captive bred populations may 'rapidly undergo significant evolutionary change' in their morphological, behavioural, and physical makeup that may have a negative impact on fitness under natural conditions (Arnold 1995; Lynch and O'Hely 2001; Araki *et al.* 2009). In such situations, there may be a 'carry-over effect' of the captive breeding into the wild that has the potential to reduce reproductive fitness within the offspring of free-ranging species, including that of subsequent generations. Araki *et al.* (2009) observed this phenomenon in steel-head trout *Oncorhynchus mykiss*. Overall relative reproductive fitness in wild-born fish from captive-bred parents was 37% while those from one captive-bred parent and one wild-bred parent was 87% of that of offspring from two wild-bred parents.

A factor that directly affects the viability of captive-bred individuals that are released into the wild is their chance of survival. After an extensive review of the literature, Jule *et al.* (2008) concluded that survivorship success in captive-bred carnivores compared to individuals born in the wild and translocated varied. Across five families and 17 species of captive-bred carnivores, significantly fewer were likely to survive in the wild than wild-born individuals. Captive-bred individuals were more susceptible to starvation, unsuccessful predator and/or competitor avoidance, and disease, although over 50% of all fatalities were directly caused by humans.

Biodiversity restoration or community driven single-species management of favoured species?

Throughout this paper, I have written of 'single-species management' (cf. Simberloff 1998). All of the Australian species mentioned would fall under the definition of one or more of the widely used terms – 'charismatic megafauna' and 'flagship' species (see e.g., Leader-Williams and Dublin 2000). For example, the koala would definitely be considered 'charismatic megafauna', while mammals

are often referred to as 'flagship species', although the term may also incorporate any of the popular, charismatic species, and Leader-Williams and Dublin (2000) noted that the terms were often used interchangeably.

The term 'flagship', and by association, other such terms indicating 'iconic' status for a species was apparently first used by conservationists in the mid-1980s (Mittermeier 1988; Western 1987; Leader-Williams and Dublin 2000) to raise awareness for the conservation of the golden lion tamarin *Leontopithecus rosalia* in Brazil. The conservation of this species did play the broader role of conservation of biodiversity, presumably because their conservation was inexplicitly linked to their rainforest habitat (Mittermeier 1988; Dietz *et al.* 1994; Mittermeier *et al.* 2005).

No matter which of the numerous terms are used to identify iconic species (cf. Leader-Williams 2000), they are considered to be symbols or 'rallying points to stimulate conservation awareness and action' and financially support conservation of the associated species' habitat and thus, indirectly, support biodiversity conservation within the species' range. For example, primates have been considered the best flagship species for entire regions (Mittermeier 1988; Dietz *et al.* 1994; Mittermeier *et al.* 2005).

In the words of Duka and Masters (2005 p. 172), the koala has a 'high and favourable social profile and appeals to a wide variety of people, particularly overseas visitors', and it has frequently been described as a 'flagship' species (Penn *et al.* 2000; Barua *et al.* 2011; Cristescu 2011) and/or as 'charismatic megafauna' (Feldhamer *et al.* 2002; Barney *et al.* 2005; Tisdell and Nantha 2007). Arguably the species has gained this iconic status in recent decades due largely to vocal and emotional community outpourings that have driven species and ecosystem management of the species, despite contrary scientific advice (Jackson 2007; Melzer 2009). However, not all native species are afforded the same level of concern. For example, both the western grey kangaroo *Macropus fuliginosus* (Cheal 1986; Arnold *et al.* 1989; Duka and Masters 2005) and the tammar wallaby *Macropus eugenii* (Wright and Scott 1999; Chambers and Bencini 2000) are culled, and kangaroo harvesting (i.e., culling) is considered a successful management option (e.g., Caughley *et al.* 1987; Arnold 1988; Grigg 1988, 1995), although the program has had detractors (e.g., Arnold 1988; Stacker 1988; Hale 2004).

In contrast to the lack of successful intervention in macropod culling on Kangaroo Island (Wright and Scott 1999), the decision to cull koalas on the Island because of their 'pest status' in late 1970s (Masters *et al.* 2004), met with 'strong adverse reaction'. Although no surveys were undertaken of community attitudes, based on unsolicited feedback to governments, the koala management program was restricted to sterilisation and translocation (Duka and Masters 2005), although humane culling of tammar wallabies was being undertaken on the Island at the time without vocal resistance (Wright and Scott 1999).

When the koala management program commenced in 1997, the founder population of 18 koalas translocated to Kangaroo Island between 1923 and 1925 was estimated to be 5,000 although this was later deemed to be a substantial underestimate. Some years after implementation of the management regime, when surveys were undertaken in 2000-2001, the original estimates were confirmed to be erroneous. As a result, the estimate of koalas was revised upwards to approximately 27,000. There were also no scientific controls implemented at the beginning of the program and thus interpretation of the results of the program has been problematic (Maters *et al.* 2004). These shortcomings provide an indication of the extent to which political pressure, rather than scientific method, prevailed in this program. Duka and Masters (2005) reported that they agreed with criticism of the program for such reasons. They also considered that the program was expensive, and did not address the longer term management of the species. Clearly, the program will not satisfy either the management of koalas, or the restoration of biodiversity including genetic biodiversity on the island. The role of 'flagship' has; therefore, failed both the species and the biodiversity of the Island more generally. Resources spent on the program could have been better diverted to more lasting biodiversity restoration outcomes.

In other ways, koalas have not proved to be a great 'flagship' species for biodiversity restoration. For example, in fragmented agricultural landscapes, koalas were found to spend more of their time in four to seven year old eucalypt plantations than in adjacent natural areas, presumably because of a ready supply of eucalypt leaves - food which is not typically included in the diet of other native arboreal marsupials of the area. Koalas also do not require diurnal shelter and breeding sites in tree hollows that most species of the native arboreal marsupials require (Kavanagh and Stanton 2012). Focusing on managing for the 'flagship' koala in the study area is, therefore, unlikely to have beneficial outcomes for the local biodiversity more generally. Indeed, the logical outcome of the research based narrowly on the findings of the needs of the flagship species (i.e. koala) would logically be to expand the eucalypt plantations.

Conclusions

The approach to native biodiversity restoration, as currently managed, is not maximising the potential outcomes that could be achieved over the longer term. A fundamental issue is the lack of a clear understanding of the word 'biodiversity'. There is a need to recognise the centrality of genetic biodiversity within the definition of biodiversity and thus in the management of species. In the longer term, any 'successful' restoration program that ignores the importance of genetic biodiversity will be largely due to chance. This will be the situation, whether the restoration

efforts are based on captive breeding or the management of populations within the wild. It is not that the importance of genetic biodiversity is unknown. Rather it is considered complex, is typically unobservable, and often not explicitly acknowledged in biodiversity restoration, even when the fundamental principles are carefully incorporated.

While those who work, teach and/or undertake research within the area of biodiversity do not emphasise its importance, even within definitions of the word 'biodiversity', it is logical that policy makers and the broader community will not acknowledge its importance or even be aware of it. For example, the Lord Howe Island woodhen went from the brink of extinction to 200 birds in a captive breeding program between 1980 and 2007 (DECC 2007). However, I suggest that in terms of genetic biodiversity it would have been a much more modest gain, and probably none. Likewise a trip to Taronga Zoo provides the visitor with exposure to information on the thousands of corroboree frogs bred at the zoo. Based on the published surveys of the genetic diversity of the species, and because the breeding is being undertaken under the auspices of the Zoo who have well developed breeding programs for a range of species, it could be assumed that the best science has been incorporated into this program. However, what would capture most visitors' attention is the large number of iconic frogs that have been bred. However, what is not observed are the issues, some outlined above, which potentially accompany captive breeding. Few people who visit Taronga Zoo without knowledge of the genetic pitfalls of captive breeding, but engage with the corroboree frog exhibit, would leave without having a positive view of the program. Many probably would leave viewing the concept of captive breeding as an appropriate approach to biodiversity restoration. Some may even become advocates for captive breeding. This is not surprising since it is an impressive program and the species is viewed as endangered and iconic.

As a consequence of being convinced of the success of such biodiversity restoration projects, governments may bow to pressure from the community, and even offer substantial resources for biodiversity restoration that may, in the extreme, have no real benefit for the targeted species and maybe even a detrimental effect on the species over the longer term. Indeed, it may also be at the expense of other, more appropriate approaches to biodiversity restoration for populations of the same species and/or for other species that may be evolutionarily more important, but are bypassed due to lack of resources. As a consequence biodiversity continues to unnecessarily erode. For example, due to public pressure, although without a quantitative assessment of opposition or even a comprehensive assessment of the number of koalas on the Island, individuals of an inbred population on Kangaroo Island were sterilised and released/translocated. The

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program, as devised, could not address the real issue over the longer term – the super-abundance of koalas on the Island, or the associated damage that they were having on their food species, and thus the Island's flora and fauna that were being affected by their super-abundance. However, instead of addressing these issues, the funds were effectively wasted and thus the habitat of other native species on Kangaroo Island continued to be degraded by the genetically depurate superabundant population of koalas.

This was typical of a situation where scientific knowledge has been over-ruled to 'save' the 'charismatic iconic'/'flagship' species. However, although species such as koalas are touted as the saviour of biodiversity, in the sense of the long-term management of the ecological diversity of Kangaroo Island, it was because it was an iconic species that the koala has had effectively the opposite effect. Rather than its presence supporting biodiversity restoration of Kangaroo Island,

nothing has been achieved in terms of even the long-term management of the koala.

Arguably the greatest issue associated with incorporating genetics more centrally into biodiversity restoration is that the definition of biodiversity is often considered to be complex, whereas the negative aspects of biodiversity restoration may appear to be positive when the outputs introduce a species or boost numbers of a species that has been deemed to be at risk of extinction despite the longer term outcomes potentially having the opposite effect. I suggest that the way forward is for all those of us who encompass biodiversity restoration within our discipline areas to redouble our efforts to ensure that, wherever possible, we seek to inform those around us of the importance of genetic biodiversity. In doing so, it would be useful if we could make it a matter of priority to develop a simple, all-encompassing definition of biodiversity that explicitly includes genetics along with the other levels of diversity.

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